

Pine

# SEASONAL FINE-ROOT CARBOHYDRATE AND GROWTH RELATIONS OF PLANTATION LOBLOLLY PINE AFTER THINNING AND FERTILIZATION<sup>1</sup>

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**Abstract**—In 1989, two levels each of stand density and fertilization were established in an 8-year-old loblolly pine (*Pinus taeda* L.) plantation. In March 1995, treatments were reapplied, and root elongation and carbohydrate concentrations were monitored for 2 years. Our objective was to evaluate relationships between seasonal root growth and carbohydrate concentration in response to thinning and fertilization. Peak root elongation occurred between May and July. Root elongation was greater in response to thinning throughout 1995 and, although not always significant, was consistently greater in thinned plots in 1996. Root growth was reduced in the fertilized plots throughout 1996. Positive effects of thinning on fine-root starch concentrations were observed. Starch levels were consistently lower in response to fertilization for most of 1995 but were greater in fertilized plots during winter 1996. Glucose levels tended to be greater in response to thinning both years and less in response to fertilization in 1995. We conclude that fine-root carbohydrate concentration and net root elongation are characterized by distinct seasonal patterns, and that the magnitude of seasonal root elongation and carbohydrate concentrations is influenced by silvicultural treatments.

## INTRODUCTION

Loblolly pine (*Pinus taeda* L.) is of significant economic importance in the southern United States (Schultz 1997). Many abiotic factors, such as moisture, fertility, and light, limit the growth of this species (Allen and others 1990, Teskey and others 1994a). Roots supply the essential water and mineral nutrients needed for growth. Thus, the ability of tree root systems to supply these resources affects stand productivity (Cropper and Gholz 1994, Eissenstat and Van Rees 1994).

The production of new roots in forest stands may increase or decrease in response to silvicultural treatments such as thinning and fertilization (Sword and others 1998a, 1998b, Albaugh and others 1998). Root-growth responses to silvicultural treatments have been linked to changes in leaf area, carbon fixation, and photosynthate allocation to the root system (Albaugh and others 1998, Gower and others 1992). Since new root growth is regulated, in part, by carbohydrate availability in the root system (Kozłowski and Keller 1966, Noland and others 1997), knowledge of how silvicultural treatments affect root carbohydrate relations is needed to understand how root growth is manipulated by these treatments.

Our objective was to evaluate relationships between seasonal root growth and carbohydrate relations of plantation loblolly pine in response to thinning and fertilization. We hypothesized that: (1) seasonal patterns of fine-root starch and glucose concentrations are closely related to new root growth, and (2) manipulation of stand density and soil fertility affects the relationship between fine-root starch and glucose concentrations and root growth.

## MATERIALS AND METHODS

This study was conducted in a 14-year-old loblolly pine plantation on the Palustris Experimental Forest in Rapides Parish, LA. The soil is a Beauregard silt loam that is low in available phosphorus (Kerr and others 1980). Genetically unimproved, container-grown loblolly pine seedlings were planted in 1981 at 1.8- x 1.8-m spacing. In 1988, 12

treatment plots, 13 rows of 13 trees each (0.06 ha), were established. Two levels of fertilization (none; 744 kg ha<sup>-1</sup> diammonium phosphate) in April 1989 and two levels of thinning (none: 2990 trees ha<sup>-1</sup>; row thinned: 731 trees ha<sup>-1</sup>) in November 1988 were randomly applied in a two-by-two factorial design with three replications. In March 1995, fertilization (none; 444 kg urea + 248 kg triple super phosphate + 100 kg potash ha<sup>-1</sup>) and thinning (none: 42 m<sup>2</sup> ha<sup>-1</sup>; 15.6 m<sup>2</sup> ha<sup>-1</sup>) were reapplied.

Two of the three replications were blocked by topography. Precipitation was quantified electronically in a clearing approximately 25 m from the study. Volumetric soil water content of the 15-cm depth was measured biweekly at three locations per plot of each replication using time domain reflectometry.

Using previously described methods, net root elongation (mm dm<sup>-2</sup>) in five Plexiglas rhizotrons per plot of two replications was quantified on a biweekly basis between April 1995 and March 1997 (Sword and others 1996, Sword and others 1998b). Root elongation from April 1995 through February 1996 is also reported elsewhere (Sword and others 1998b).

At 2- to 4-week intervals, 10 soil cores (6.5 cm x 15 cm) were extracted from random locations in the periphery of each plot of two replications using a metal coring device (Ruark 1985). Branched fine-roots ( $\leq 1.0$ -mm diameter) were elutriated from soil cores (Smucker and others 1982). Roots from each plot were pooled, washed, frozen (-80 °C), lyophilized, and ground (40-mesh). Fine-root starch and glucose concentrations were determined using a modification of the procedure described by Jones and others (1977). Starch and soluble sugars were extracted from 25 mg ground root tissue and enzymatically converted to glucose. Glucose was quantified by the glycolytic production of reduced nicotinamide adenine dinucleotide phosphate (NADPH). Spectrophotometrically, NADPH was measured at 320 nm. Carbohydrate concentrations are expressed as mg g<sup>-1</sup> ash-free dry weight.

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(harvested and standing) number of trees as compared to the unthinned control. This thinning "shock" (Harrington and Reukema, 1983) is most significant for basal area and less so for number of trees and dominant height.

Twelve years after thinning the thinned plot total basal area production has achieved that of the unthinned controls; total number of trees (harvested and standing) is greater than those in the controls and dominant stand height is not different between the control and thinned plots. Three years after a second thinning a similar comparison shows that the dominant height, total basal area and total number of trees has surpassed the unthinned control. For dominant height and number of trees the difference is significant. Thus it appears that there is little, if any "shock" associated with the second thinning. The significant difference in dominant height three years after the second thinning is due in part to the selection effects of two low thinnings which removed some of the smaller codominant trees. That plus the faster growth from larger, better quality residual trees has produced a statistically significant, but rather small (about one foot) increase in average dominant height on these twice-thinned plots.

The analysis of covariance evaluation of three-year growth following first and second thinnings shows a significant difference in dominant height and basal area increment as well as mortality. For dominant height and basal area, these differences imply that the negative impact of post-thinning "shock" on growth was significantly greater for the first thinning than for the second. There was significantly less mortality for the three-year period following the second thinning than following the first.

When assessing the results of this study, it should be remembered that:

1. Only the response in the first three year period following thinning could be evaluated. It is not clear how longer elapsed time since treatment might affect a comparison between first and second thinnings.
2. Data were only available for two thinnings spaced twelve years apart. It is not apparent what effect additional thinnings or thinnings that occur closer together or farther apart in time might have on the analyses.

The results found in this study should be helpful to modelers who are developing equations for predicting response to thinning treatments. When modeling growth following thinning, it should be possible to develop more precise models by differentiating first from second (and subsequent) thinnings.

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New root elongation and root carbohydrate data at each measurement interval were transformed ( $\log[Y+1]$ ) as needed to establish normality and subjected to an analysis of variance using a randomized complete block design with two replications. Main and interaction effects were considered statistically significant at probabilities ( $Pr$ )  $\leq 0.05$ .

## RESULTS

From January through June 1996, precipitation was 76 percent less than during the same period in 1995 (fig. 1). During the growing season (May–November) and period of maximum root elongation (May–July), reductions in precipitation of 22 and 30 percent, respectively, were observed in 1996 when compared to 1995. For the periods extending both from May through July and May through November, the mean soil water content at 15 cm was 20 percent less in 1996 than in 1995.

During the 1995 growing season (May–November), 70.0 percent of the root elongation occurred from May through July, and 28.5 percent occurred from August through November (fig. 2). In 1996, 42.2 and 46.3 percent of root elongation occurred from May through July and August through November, respectively.

As reported by Sword and others (1998b), root elongation was positively and significantly affected by thinning throughout 1995. This trend was consistent during the 1996 growing season, although only significant in May (fig. 2). Root elongation was not affected by fertilization in 1995 (Sword and others 1998b) but was significantly reduced by fertilization during most of 1996.

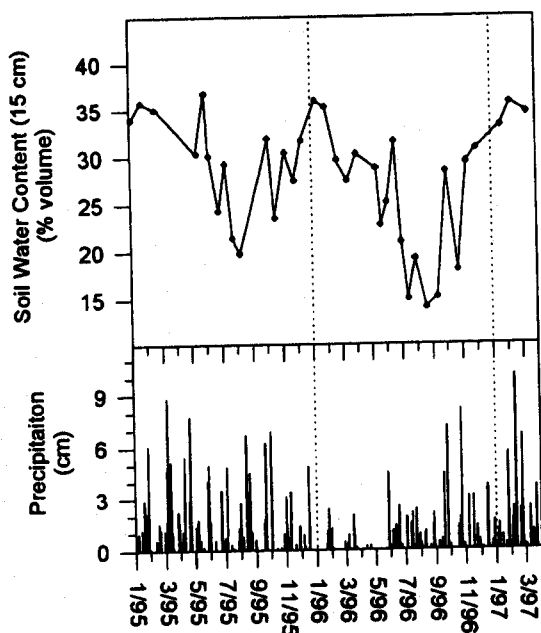


Figure 1—Percent volumetric soil water content at 15 cm (A) and daily precipitation (cm) (B) in 1995 and 1996.

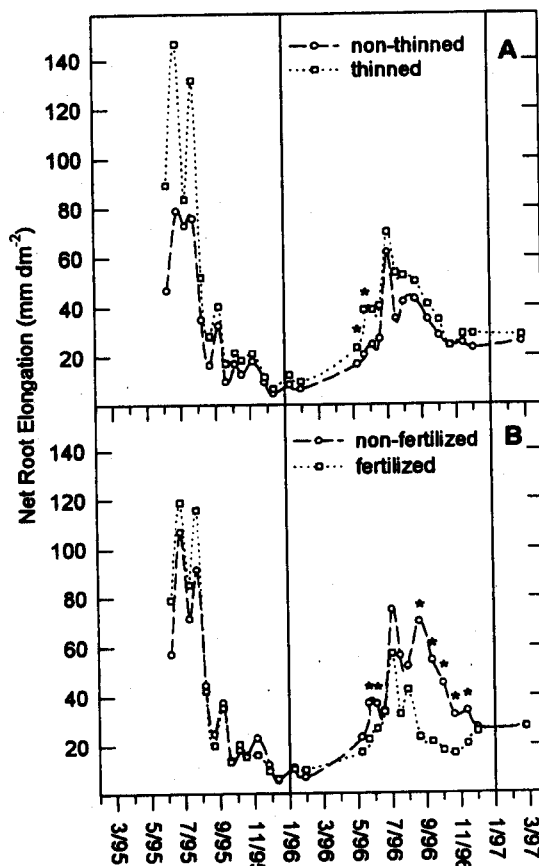


Figure 2—Net root elongation of loblolly pine ( $\text{mm dm}^{-2}$ ) by thinning (A) and fertilization (B) treatments in 1995 and 1996. As reported by Sword and others (1998b), root elongation was positively and significantly affected by thinning throughout 1995–96. An asterisk (\*) indicates statistical significance at  $Pr \leq 0.05$  on measurement dates in 1996–97.

The seasonal pattern and magnitude of fine-root starch concentration were similar in 1995 and 1996 (figs. 3 and 4). In both years maximum concentrations of fine-root starch were observed in March and April, and minimum concentrations from July through November. The seasonal pattern of fine-root glucose concentration was similar in 1995 and 1996; minimum concentrations occurred from January through May and progressively increased during June and July. Maximum fine-root glucose concentration in 1995 and 1996 was observed in August through October and August through December, respectively.

During the period of maximum fine-root glucose concentration in 1995 and 1996, the magnitude of concentration differed. From August through October 1996, the fine-root glucose concentration was 16 percent greater than from August through October 1995.

Fine-root starch concentration was generally greater in response to thinning between March 1995 and February 1997 (fig. 3a); however, statistical significance was sporadic

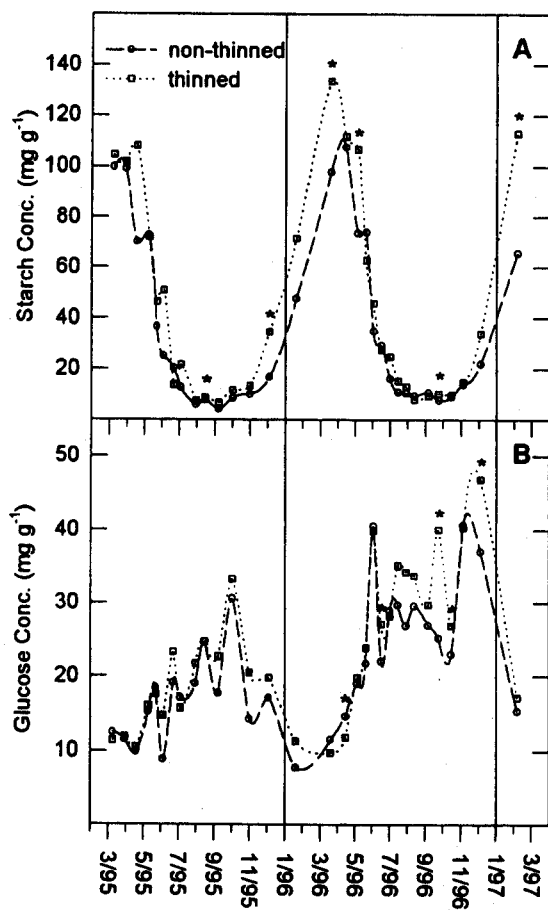


Figure 3—Fine-root starch (A) and glucose (B) concentration ( $\text{mg g}^{-1}$  ash-free dry tissue) by thinning treatment in 1995 and 1996. Thinning was a statistically significant effect ( $P \leq 0.05$ ) on measurement dates noted with an asterisk (\*).

(table 1). Fine-root glucose concentration was not significantly affected by thinning in 1995 (fig. 3b). In mid-April 1996, however, the concentration of glucose in fine-roots was significantly lower, and in mid-June and three times in the fall of 1996, was significantly greater in response to thinning (table 2).

In 1995, before starch accumulation began in November, fine-root starch concentration was consistently lower in response to fertilization with intermittent significance (table 1, fig. 4a). This response was reversed in March 1996. Fine-root glucose concentration was significantly lower in response to fertilization from August through November 1995 and April 1996 (table 2, fig. 4b). After April 1996, fine-root starch and glucose concentrations were not significantly affected by fertilization.

## DISCUSSION

Fine-root starch concentration was modal with periods of accumulation from December through March and depletion from April through July. Minimum starch concentration was

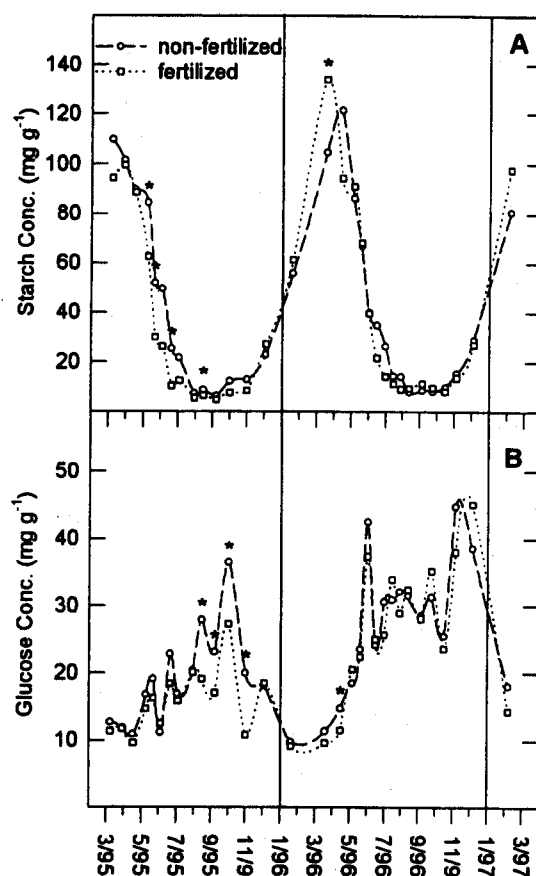


Figure 4—Fine-root starch (A) and glucose (B) concentration ( $\text{mg g}^{-1}$  ash-free dry tissue) by fertilization treatment in 1995 and 1996. Fertilization was a statistically significant effect ( $P \leq 0.05$ ) on measurement dates noted with an asterisk (\*).

maintained from August through November. These results are consistent with other observations of southern pine species (Adams and others 1986, Gholz and Cropper 1991). Teskey and others (1994a) suggested that substantial photosynthesis continues throughout winter in warm climates. Our results indicate that, during winter root, starch is a sink for photosynthate in plantation loblolly pine.

Based on the results of seedling experiments, newly translocated photosynthate is considered the primary source of energy for conifer root growth rather than stored starch (Ritchie and Dunlap 1980, van den Driessche 1987). If the availability of current photosynthate is limited, however, a greater portion of stored starch may be used as an energy source for root growth (Noland and others 1997, Philipson 1988). In both 1995 and 1996, fine-root starch concentration decreased between March and June, while net root elongation increased between May and July. Although fine-root starch concentration was near its lowest level, fine-root glucose concentration was relatively high in July. This suggests that starch and current photosynthate provided the

**Table 1—Probability of a greater F-value associated with significant effects on the fine-root starch concentration ( $\text{mg g}^{-1}$ ) of 16-year-old loblolly pine from March 1995 through February 1997 in response to two levels each of thinning and fertilization**

Variable	df	Probability > F-value						
		Measurement dates						
		1995						
		5-11	5-23	6-22	8-17	9-8	11-3	12-11
Block (B)	1	0.8297	0.2327	0.2196	0.0232	0.5252	0.7893	0.8011
Thinning (T)	1	.6373	.3291	.0854	.0190	.0866	.2430	.0056
Fertilization (F)	1	.0009	.0508	.0082	.0044	.3030	.0595	.8763
T x F	1	.8867	.3977	.0183	.0041	.8593	.7425	.8398
		1996						
		1-25	3-20	5-7	8-13	9-24	10-16	1997 2-6
Block (B)	1	.2863	.1100	.7001	.0181	.6289	.5612	.5440
Thinning (T)	1	.0841	.0126	.0031	.1011	.0194	.2629	.0093
Fertilization (F)	1	.7659	.0222	.5471	.0650	.1298	.0781	.1207
T x F	1	.1980	.3592	.0200	.1645	.8650	.8115	.0497

**Table 2—Probability of a greater F-value associated with significant effects on the fine-root glucose concentration ( $\text{mg g}^{-1}$ ) of 16-year-old loblolly pine from March 1995 through February 1997 in response to two levels each of thinning and fertilization**

Variable	df	Probability > F-value					
		Measurement dates					
		1996					
		7-6	8-17	9-8	9-25	11-3	
Block (B)	1	0.1912	0.8104	0.1758	0.0100	0.3764	
Thinning (T)	1	.0817	.1530	.0734	.2230	.1823	
Fertilization (F)	1	.1666	.0362	.0364	.0125	.0102	
T x F	1	.0086	.0410	.5477	.0201	.1467	
		1996					
		4-16	6-17	7-30	9-24	10-16	12-5
Block (B)	1	.0227	.7550	.1861	.6035	.0459	0.1136
Thinning (T)	1	.0328	.0486	.0706	.0303	.0106	.0337
Fertilization (F)	1	.0176	.6060	.3226	.7008	.1667	.0894
T x F	1	.0873	.1713	.3328	.3485	.0450	.0867

glucose for root elongation through June. In July, however, after starch reserves were depleted, root elongation proceeded, primarily with glucose supplied by current photosynthate. Sword and others [in press] reported that fine-root sucrose concentrations remained relatively constant from March 1995 through January 1996. It is believed that both starch and current photosynthate are sources of energy for loblolly pine root metabolism during the period of maximum root elongation. However, the relative contributions of starch and current photosynthate to root metabolism during this period cannot be determined by this study.

Past research has shown a positive relationship between light availability to the shoot and root carbohydrate concentration in pine (Noland and others 1997, Shiroya and others 1966). With a reduction in stand density, greater light availability in the forest canopy may have resulted in more photosynthate production (Peterson and others 1997), and carbohydrate allocation to root growth (Sword and others 1998b). In 1995, elevated root carbohydrate concentrations corresponded to a distinct increase in root elongation in response to thinning. Similar root-growth responses to thinning were observed in 1993 and 1994 (Sword and others 1998a, 1998b). Positive stand-productivity responses to

thinning have been attributed to increases in light availability and carbon fixation in the canopy, and carbon allocation to diameter growth (Kozlowski and others 1991). On sites where tree growth is limited by the availability of water or mineral nutrients, thinning may also enhance stand productivity by increasing carbon allocation to root growth and, therefore, soil resource uptake.

Fertilization had a negative effect on root elongation in 1996, but no effect in 1995. Absence of an effect in 1995 was not unexpected, because the effect of fertilizer application in 1989 on root elongation was negligible by 1993 and absent by 1994 (Sword and others 1998a, 1998b). Also, starch and current photosynthate availabilities for root metabolism and growth in 1995 were defined by leaf-area attributes established before fertilizer was reapplied. Specifically, foliage produced in 1994 was the source of starch that accumulated in fine-roots from December 1994 through March 1995. Also, carbon gains after fertilization are attributed, in part, to an increase in leaf area (Teskey and others 1994b, Vose and Allen, 1988). Because the fascicle density of the first flush is determined during terminal bud development in the previous year (Stenberg and others 1994), leaf area and, therefore, the amount of photosynthate produced on the fertilized plots in 1995, could not have been strongly affected by the reapplication of fertilizer in March 1995.

Past research has shown that nitrogen fertilization causes a shift in the proportion of photosynthate allocated to aboveground and root-system growth (Albaugh and others 1998, Gower and others 1992). Albaugh and others (1998) found that for 9- to 12-year-old loblolly pines, average annual biomass allocation was 14 percent greater to aboveground tissues and 63 percent lower to fine-roots in response to fertilization. Our results demonstrate a similar response to fertilization. In July 1995, after starch was depleted from fine-roots and current photosynthate became the primary energy source for root growth, fertilization resulted in a lower concentration of fine-root glucose but did not affect root elongation. In 1996, a similar fine-root glucose response to fertilization was not observed, but fertilization resulted in less root elongation. We hypothesize that less photosynthate was allocated to the root system on fertilized plots than to the root system on non-fertilized plots, resulting in a reduced concentration of fine-root glucose in 1995 and reduced root elongation in 1996.

These results indicate that during the growing season, fertilization reduced photosynthate allocation to the root system; although during the dormant season (December through March), photosynthate allocation to roots appeared to respond differently. Termination of branch growth and continued photosynthesis in winter, together with an increase in leaf area per tree in response to fertilization, may have led to the observed increase in fine-root starch concentration in March. Thus, the presumed negative effect of fertilization on carbon allocation to the root system may not apply during the accumulation of starch in the dormant season.

Past research has shown that root elongation in loblolly pine is sensitive to water availability (Ludovici and Morris 1996). Sword and others (1998a, 1998b) observed that the seasonal reduction in root elongation during July 1993 and 1994 coincided with reduced soil water content. In this study, the magnitude of root elongation was less in 1996

than in 1995. This reduction was associated with an unusually dry winter and spring. Limited soil water availability from May through July 1996 may have inhibited root elongation. The seasonal pattern of root elongation in 1996 was also different from what was reported between 1993 and 1995 (Sword and others 1998a, 1998b). More root elongation occurred from August through November in 1996 than during the same period in previous years. After an extensive period of reduced water availability from January through August 1996, sufficient precipitation resumed in September. Expansion of the loblolly pine root system network by root elongation is generally restricted to May through July (Sword and others 1998a, 1998b). The seasonal pattern of root elongation observed in 1996 suggests that if root elongation is inhibited from May through July, a portion of the forfeited root system expansion can potentially be recovered between August and November.

Reduced water availability may have prompted the 54 percent increase in fine-root glucose concentration between 1995 and 1996. Because maintenance of a high solute concentration in root cells increases their hydration by osmosis (Kramer 1983), storage of glucose rather than starch may have been a physiological mechanism of drought tolerance. Storage of root carbohydrates as glucose rather than starch may also have been an energy conservation strategy by which glucose was a readily available source of energy for rapid root growth in the event of precipitation.

## SUMMARY

Root-starch reserves in plantation loblolly pine appear to be a carbohydrate sink during the dormant season. These reserves may be a source of energy for loblolly pine root metabolism early, when maximum root elongation is occurring. Thinning was beneficial to starch accumulation and the growth of fine roots. On sites where tree growth is limited by the availability of water or mineral nutrients, thinning may enhance stand productivity by increasing carbon allocation to root growth and, therefore, soil resource uptake. Generally, nitrogen fertilization had a negative effect on carbon allocation to loblolly pine roots except during the dormant season, when starch accumulation increased in response to fertilization. Limited soil water availability from May through July 1996 appeared to inhibit root elongation. However, root elongation resumed later in the growing season, as water became available.

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